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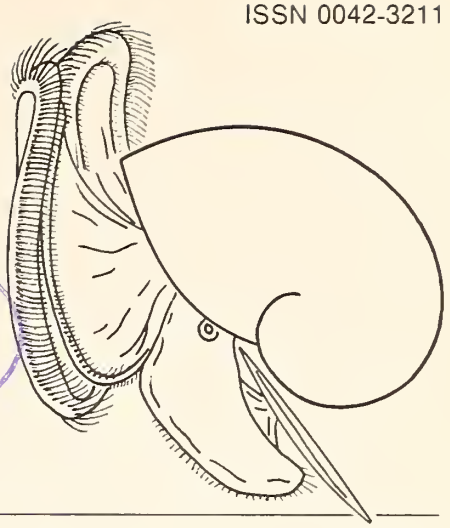
THE VELIGER



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THE VELIGER

The Functional Morphology of the Pedal Musculature of the Marine Gastropods *Busycon contrarium* and *Haliotis kamtschatkana*

by

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Abstract. The gastropod foot shows a high degree of morphological complexity and behavioral plasticity. This study describes the arrangement of the muscle fibers and connective tissue in the feet of *Busycon contrarium* and *Haliotis kamtschatkana* and analyzes the functional roles of the various muscle groups in wave propagation and other pedal actions. In addition, it presents the role of the connective tissue as an essential element in pedal function. The prosobranch foot is primarily solid muscle: it consists of two structurally and functionally distinct regions, the columellar muscle and the tarsos. The region of the columellar muscle consists of thick bundles of muscle fibers wrapped in connective-tissue sheaths and arranged in an orthogonal latticework. The muscle fibers of this region perform the gross shell-foot movements: protrusion, retraction, shell elevation, and twisting. The tarsos also consists of bundles of muscle fibers wrapped in connective-tissue sheaths. In this region, however, large bundles from the dorsal portion of the region divide into finer and finer branches as they approach the sole and sides of the foot, forming a network of small groups of muscle fibers embedded in a dense connective-tissue matrix. This muscle system is responsible for the finer movements of the foot, including propagation of locomotor waves, manipulation of prey, and formation of egg capsules. In both regions, the connective tissue, by transmitting compressive and tensile forces, probably provides the mechanism by which one set of muscle fibers can directly antagonize another.

INTRODUCTION

The gastropod foot is a fleshy, flexible organ that performs a diversity of functions. Besides locomotion and adhesion, a snail can also use its foot to capture and consume prey, to mate, to shape and deposit egg capsules, to clean its shell, and to thwart potential predators.

Although the external characteristics of the gastropod foot have been thoroughly described and classified (Vlès, 1907; Miller, 1974a, b; Gainey, 1976) there are relatively few studies of the internal organization, and even fewer that relate structure to function: Trappmann (1916) described the arrangement of the musculature of *Helix pomatia* Linné; Rotarides (1941, 1945) described the organization of the musculature of *Nassarius mutabilis* (Linné) (=*Nassa mutabilis*) and of several limpetlike forms; Jones & Trueman (1970) described the pedal musculature of *Patella vulgata* Linné, 1758; Jones (1973) described *Agriolimax reticulatus* (=*Deroceras reticulatum* (Müller)); Plesch *et al.* (1975) described the body wall and pedal musculature of *Lymnaea stagnalis* Linné; Gainey (1976) described the pedal musculature of *Neritina reclivata* (Say, 1822) and *Thais rustica* (Lamarck, 1822); and Trueman & Brown (1976, 1985, 1987) described the pedal musculature of *Bullia digitalis* (Dillwyn) and *Haliotis midae* Linné. In most cases, however, the authors were primarily interested in identifying muscle systems and in describing the orientations of the muscle fibers within the foot.

The complicated patterns of muscular organization in the gastropod foot have prompted workers to propose several possible antagonists for the muscular contractions of pedal waves. Jordan (1901, 1905) believed that the pressure of the blood in the lacunae extends the relaxed muscle in the foot of *Aplysia limacina*. Trappmann (1916) suggested that the transverse muscle fibers provide the necessary antagonistic force in *Helix pomatia*. Simroth (1878) proposed that the muscle fibers involved in locomotion actively expand, as well as contract. Separate explanations

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have been proposed for the mechanisms of direct and retrograde wave propagation and for burrowing (see TRUEMAN [1983] for review).

A hydrostatic skeleton is any "fluid mechanism which in one way or another provides a means by which contractile elements can be antagonized" (CHAPMAN, 1958). Because the only requirements are that the fluid be fairly incompressible and transmit pressure in all directions, a variety of different fluids including water, blood, mesoglea, or coelomic fluid, might serve this function. In most of the models of gastropod locomotion, the blood serves as the antagonist to muscular contraction. The blood has been proposed as a fluid skeleton in *Lymnaea stagnalis* (BEKIUS, 1972), *Haliotis* spp. (CROFTS, 1929), *Helix pomatia* (DALE, 1973), *Agriolimax reticulatus* (=*Deroceras reticulatum*) (JONES, 1973), and *Patella vulgata* (JONES & TRUEMAN, 1970), although, in the last example, what were originally identified as hemocoelic vesicles have been demonstrated to be mucous glands (GRENON & WALKER, 1978, 1982). The principle upon which these models are based was introduced by PARKER (1911) in a review of JORDAN (1901) and BIEDERMANN (1905): "The musculature of the snail's foot works against the elastic-walled, fluid-filled cavities of the animal's interior."

VOLTZOW (1985), however, demonstrated that the "open" circulatory system of the foot of the marine prosobranch *Busycon contrarium* (Conrad, 1840) consists of discrete arteries and veins that anastomose throughout the foot in a pattern resembling the "closed" circulatory system of annelids and vertebrates. A network of small spaces delimited by the surrounding muscle and connective-tissue matrix links the arteries and veins. Similar pedal circulatory systems have been observed in a diversity of other marine gastropods (Voltzow, personal observation). Thus, while probably important for expanding the sole region and for maintaining turgor once the foot has expanded, the circulatory system is not isolated from the pedal musculature. It is therefore unlikely that the blood functions as the mechanical antagonist to the muscular contractions of locomotion except in those species such as *Bullia digitalis* that have an exceptionally large fluid-filled cavity in the foot (TRUEMAN & BROWN, 1976, 1987).

As an alternative to these theories, other authors have suggested that one set of muscle fibers within the foot might directly antagonize another without any dependence upon a fluid skeleton. TRAPPMANN (1916), for example, suggested that there might be a direct antagonism between the transverse and longitudinal muscles of the foot of *Helix pomatia*. In response to the active extension mechanism proposed by SIMROTH (1878, 1879), CARLSON (1905) suggested that during the normal locomotion of *Helix dupetithouarsi* Deshayes, the contraction of the transverse and oblique muscles of the dorsal and lateral sides of the body could antagonize and extend the longitudinal muscles.

More recently, BROWN & TRUEMAN (1982) and TRUEMAN & BROWN (1985) have shown that the columellar muscle of a variety of gastropod species contains sets of transverse and radial muscles that antagonize the longitudinal muscles directly. These three-dimensional muscular antagonism systems have been called muscular-hydrostats by KIER (1982, 1988) and KIER & SMITH (1985), who have identified them in a diverse array of molluscan and vertebrate fleshy organs.

The present study investigates the nature of the gastropod pedal antagonistic system by evaluating the roles of the major structural elements—the muscle, connective tissue, and circulatory system—in two species of prosobranch gastropods, *Busycon contrarium* and *Haliotis kamtschatkana* Jonas, 1845.

MATERIALS AND METHODS

Specimens of the lightning whelk, *Busycon contrarium* (Conrad, 1840), ranging in shell length from 67 to 235 mm were collected at Beaufort, North Carolina, and Alligator Harbor, Florida, USA. Specimens of the pinto abalone, *Haliotis kamtschatkana* Jonas, 1845, were collected from San Juan Island, Washington, USA. Abalone ranged in length from 48 to 130 mm. Individuals of both sexes from both species were used. This study incorporates information gained from observations of over 50 *Busycon* and 15 *Haliotis*, as well as observations of over 20 additional species of gastropods and chitons.

Because *Busycon* is slow to emerge from its shell when disturbed, and because it retracts at any slight disturbance, I experimented with a variety of narcotization techniques. Alcohol, succinyl choline chloride, MS 222, Nembutal, propylene phenoxetol, and asphyxiation either caused snails to retract immediately into their shells or were too weak to have any effect at all. Therefore, to compare the arrangement of the musculature of expanded, crawling snails with retracted ones, some animals were frozen with liquid nitrogen as they crawled, others were narcotized most successfully with a 7.5% magnesium chloride solution, and others were fixed fresh in the retracted position.

To study the gross organization of the muscle fibers, sections several millimeters thick from fresh and fixed specimens were cut with a razor blade and traced with a camera lucida on a Wild M5 stereomicroscope. Specimens were sectioned in the sagittal, transverse, and frontal planes.

To mark the pedal circulatory system, a mixture of India ink in gelatin and water was injected into the pedal artery of smaller specimens and slices of feet. These pieces were fixed in a solution of 2.5% glutaraldehyde and 4.0% formalin in a 0.1 M phosphate buffer at pH 7.2. Experiments with fixatives of a range of osmotic concentrations indicated that this combination minimized shrinking or swelling of the tissue. The fixative's osmotic concentration was measured with a Wescor Inc. 5100C vapor pressure osmometer and adjusted to 735 mOs by adding saturated sucrose solution or distilled water. After dehydration in an alcohol series, the samples were embedded in JB-4 plastic embedding medium (Polysciences, Inc.). Sections 1–7 μm thick were cut with a Sorvall JB-4 microtome using a glass

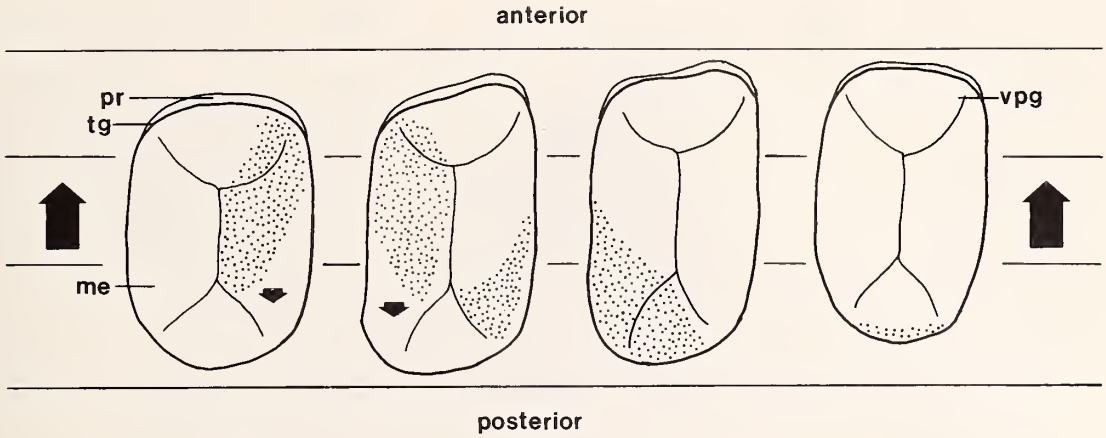

Figure 1

Diagram of the ditaxic retrograde locomotor wave pattern on the sole of *Busycon contrarium*. Large arrows indicate the direction in which the animal is moving, small arrows the direction of movement of waves. Stippled areas are those undergoing movement in each step of the passage of a wave. Pedal length varies in this species from a few millimeters to over 170 mm. me = mesopodium; pr = propodium; tg = transverse groove; vpg = ventral pedal gland.

knife. These sections were stained with toluidine blue and photographed with a Leitz Orthoplan-Pol/Orthomat polarizing photomicroscope.

Serial sections were prepared from specimens that had either been relaxed with magnesium chloride or frozen with liquid nitrogen while crawling. These were fixed in either Bouin's, Zenker's (HUMASON, 1979), or the glutaraldehyde-formalin fixative described above. After being dehydrated in alcohol and cleared in xylene or toluene, samples were embedded in Paraplast (m.p. 56-57°C), a compound of paraffin and plastic polymer, and sectioned at thicknesses varying from 5 to 10 μm. One large, whole specimen of *Busycon contrarium* was sectioned on a sliding microtome; section thicknesses ranged from 10 to 30 μm. Paraplast sections were stained with a Mallory or Milligan trichrome stain (HUMASON, 1979).

To study the detail of the entire muscular system, one specimen of *Busycon* was reconstructed photographically. The expanded foot was cut into 36 cubes, and alternate cubes were sectioned and stained. One representative section from each of 15 cubes was photographed with a compound microscope and reconstructed photographically to a final magnification of 160×. The resulting 0.5-m^2 photographic montages were suspended in a staggered array that approximated their relative positions in the foot. The entire reconstruction required over 150 pieces of 8 × 10-inch photographic paper and fills a small room.

RESULTS

Natural History Observations

Busycon contrarium lives in the intertidal and subtidal zones along the Atlantic coast from New Jersey to Florida and the Gulf of Mexico (ABBOTT, 1974). It uses an indistinct retrograde ditaxic locomotor wave to crawl on and burrow into soft substrates (Figure 1). Crawling speeds range from about 0.05 to 0.15 m/min (VOLTZOW, 1986). At the anterior end of the foot, a transverse, ciliated groove separates the propodium from the mesopodium, which is divided into anterior, left, right, and posterior fourths. During crawling, and also during periods of rest between crawling phases, the propodium undulates and probes the substrate in front of it. After a probing phase, the left and right portions of the mesopodium advance alternately by means of a faint retrograde wave of localized contraction along each side, moving the anterior portion with them. The posterior fourth of the foot then advances as if it were simply dragged along, and the cycle begins again. When burrowing, *Busycon* moves its foot ahead into the sand, then brings its shell forward over the already advanced foot. *Busycon* uses its foot to overcome, grasp, and manipulate its prey, which include slow-moving or stationary bivalves such as *Mercenaria mercenaria* (Linné, 1758) and *Crassostrea virginica* (Gmelin, 1791). It forcefully contracts its foot to chip the shell of its prey with the edge of its own shell (CARRIKER, 1951, and personal observation). Females have a ventral pedal gland that they use to give their egg capsules their final species-specific shape and to anchor them to the sand in long strings.

Haliotis kamtschatkana uses direct ditaxic waves (described by LISSMANN [1945] for *H. tuberculata* Linné) to crawl on hard substrates at speeds of over 0.2 m/min. It lives in the intertidal and subtidal zones from Japan and southern Alaska to Point Conception, California (ABBOTT, 1974) and feeds on brown macroalgae such as *Nereocystis luetkeana*. If its cephalic tentacles contact overlying pieces of algae, an abalone can rear up on the posterior portion of its foot and fold the sides of the anterior region together

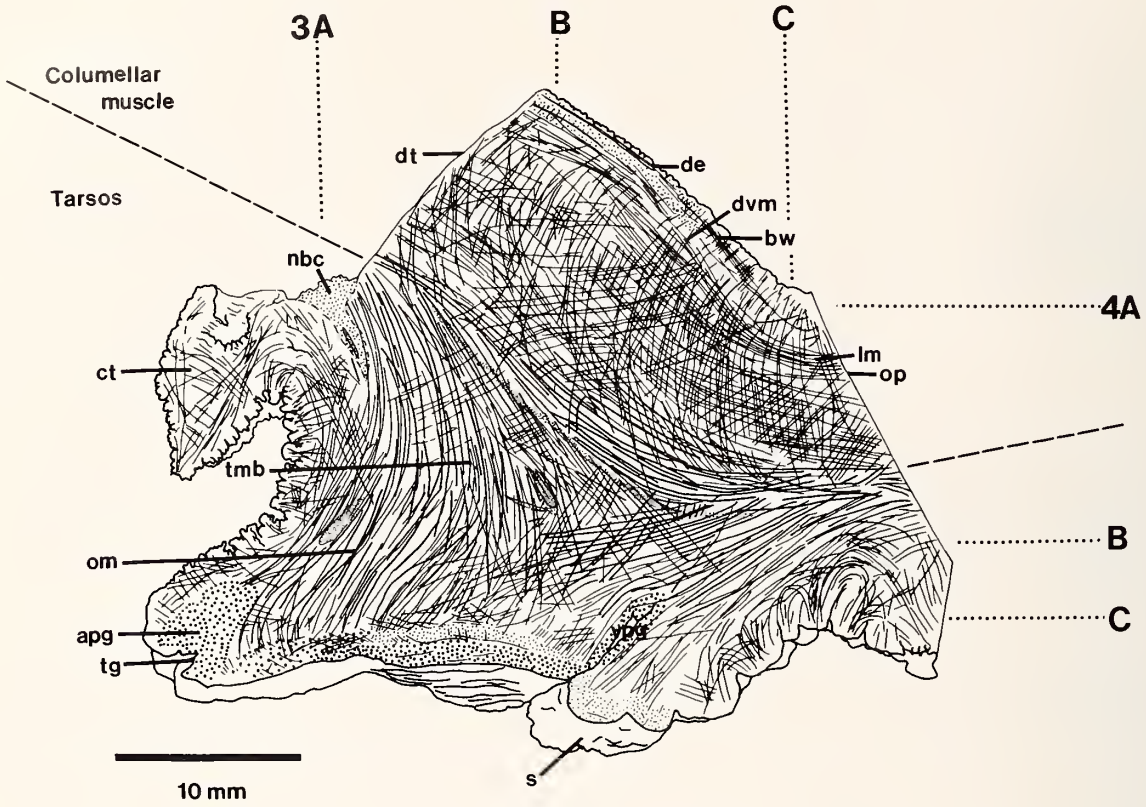

Figure 2

Camera lucida drawing of the musculature in a mid-sagittal section of a female *Busycon contrarium* head-foot. (Unless otherwise indicated, all figures are oriented so that anterior is left and dorsal is top.) Large stipple = glandular tissue; medium stipple = areas of connective tissue in which muscle fibers were too small to discern; small stipple = blood vessels; dashed lines = division between the columellar muscle region and tarsos; dotted lines = approximate positions of transverse and frontal sections of Figures 3 and 4. apg = anterior pedal gland; bw = body wall musculature; ct = cephalic tentacle; de = pedal dorsal epithelium; dt = cut margin at dorsal trunk of foot; dvm = dorsoventral muscle; lm = longitudinal muscle; nbc = nerve and blood vessel channel; om = oblique muscle; op = cut surface of operculum site; s = sole; tg = transverse groove; tmb = tarsic muscle bundles; vpg = ventral pedal gland.

like two hands to grasp the alga in a deep groove aimed at its mouth. When touched by a potential predator, such as the seastar *Pycnopodia helianthoides, Haliotis* responds by lifting and twisting its shell from side to side, clamping down on the substrate, or galloping away using locomotor waves of increased amplitude and frequency.

Pedal Musculature of *Busycon contrarium*

Internally, the *Busycon* foot consists of two distinct regions, the dorsal columellar muscle region and the ventral tarsos, which includes the sole (Figure 2). Previous studies of the gastropod foot have identified the columellar muscle but have not used any name for the rest of the foot. I have chosen the word "tarsos," which is a Greek term for the flat of the foot or a flat woven basket, to refer to this structure. In sagittal sections of fresh, protracted specimens, these two regions show distinct differences in color, texture, and shine. When touched, pulled, or chewed (sliced *Busycon* is served as "snail salad" in Rhode Island, USA), the columellar muscle is tough and the tarsos is spongy. In transverse section, the border between the columellar muscle and the tarsic region is less distinct (Figure 3). The two regions form one tightly connected entity; one cannot be lifted away from the other, for some of the muscle fibers from the columellar muscle pass into the tarsos.

Frontal sections show that the foot of *Busycon* is a meshwork of transverse, dorsoventral, and oblique muscle fibers (Figure 4). The large number of incomplete muscle fibers in any one figure indicates the extent to which the fibers are oriented obliquely to, rather than parallel to, the anteroposterior and dorsoventral axes of the foot. In section, individual muscle fibers could be called transverse, longitudinal, or dorsoventral, depending upon their orientation in the plane of the particular section. Through its entire length, however, a muscle fiber may in fact be oriented in several different directions, and these directions

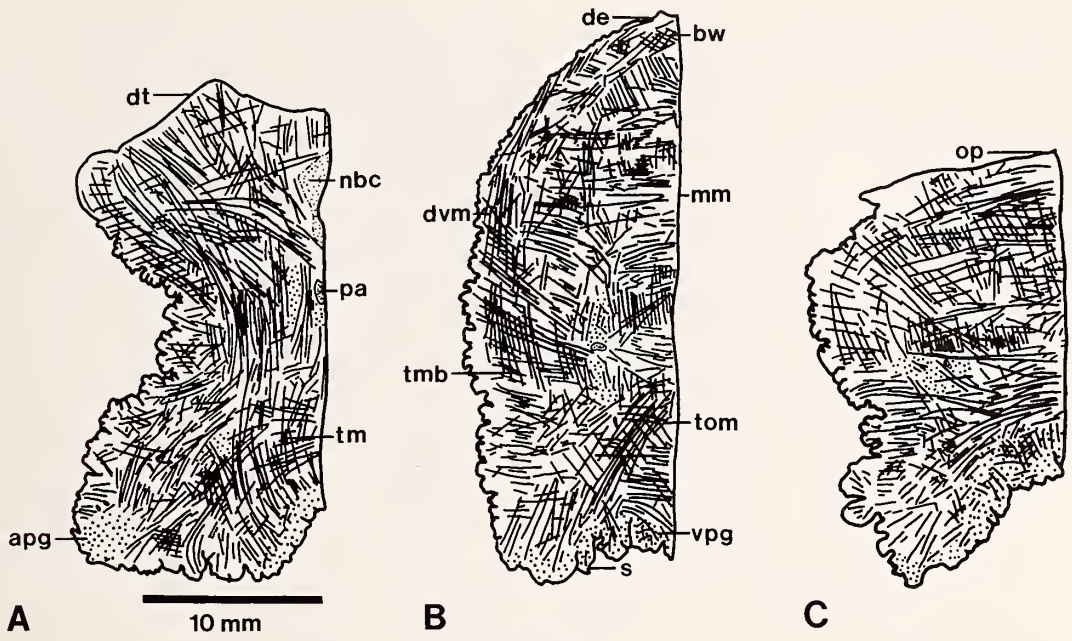

Figure 3

Camera lucida drawing of the musculature in transverse sections of a female *Busycon contrarium*. See Figure 2 for section locations in foot and explanation of stippling. apg = anterior pedal gland; bw = body wall musculature; de = pedal dorsal epithelium; dt = cut margin at dorsal trunk of foot; dvm = dorsoventral muscle; mm = cut margin at midline of foot; nbc = nerve and blood vessel channel; op = cut surface of operculum site; pa = pedal artery; s = sole; tm = transverse muscle; tmb = tarsic muscle bundles; tom = transverse oblique muscle; vpg = ventral pedal gland.

are rarely in an absolutely horizontal or vertical plane. The extent to which muscle fibers change directions can be seen by comparing the differences between sections A, B, and C of Figures 3 or 4. Within any one orthogonal section, the majority of muscle fibers are oblique with respect to the plane of section and to the epithelial surface where they insert.

The columellar muscle occupies the dorsal portion of the foot. It appears shiny and white in fresh preparations and contains a lattice of interwoven bundles of muscle fibers (Figures 2, 5). The majority (approximately 70%) of these bundles extend from the muscle's origin on the columella to its insertion on the operculum. In addition to these longitudinal fibers, within the columellar region other bundles of muscle fibers are oriented anterodorsal to posteroventral, posterodorsal to anteroventral, and directly dorsoventral (Figures 2, 5).

The dorsal border of the columellar region includes a layer of connective tissue with several thick, longitudinal muscle fibers and a scattering of thin dorsoventral muscle fibers (Figures 2, 3, 5). Dorsal to this layer, the foot is bounded by the body wall musculature (Figure 5A) and an epithelium. The ventral edge of the columellar region is delineated by a layer of shiny, parallel muscle fibers that extend anteroposteriorly from the columella to the operculum (Figure 2). The longitudinal muscle fibers of this layer are encased in thick connective-tissue sheaths and are divided into bundles by transverse and oblique muscle bundles.

The tarsos of *Busycon* consists of systems of oblique muscle fibers that interweave to form a complex three-dimensional network (Figure 6). From the surface of the anterior ventral edge of the columellar region, bundles of muscle fibers extend ventrally, branching into finer and finer units that radiate anteriorly, laterally, and posteriorly throughout the anterior two-thirds of the foot (Figure 2). These bundles eventually penetrate the sides and sole of the foot as individual muscle fibers (Figure 6E). From the surface of the posterior ventral side of the columellar muscle, similar bundles of muscle fibers divide into branches that spread anteriorly and ventrally until they, too, penetrate the sole as individual muscle fibers. In the central third of the foot, these two systems interweave.

Although not directly comparable between one animal and another (large animals tend to have relatively more thick muscle fibers, small animals tend to have relatively more thin ones), within the same animal the individual muscle fibers of the columellar region tend to have a larger diameter than those of the tarsos. Within one specimen of *Busycon contrarium* whose shell length was 95 mm, the columellar muscle fibers ranged in diameter from 3.1 to 4.4 μm. Those in the tarsos were about 1.7 to 3.4 μm. In another specimen whose shell length was approximately 150 mm, muscle fibers measured 7.4 to 11.1 μm in diameter

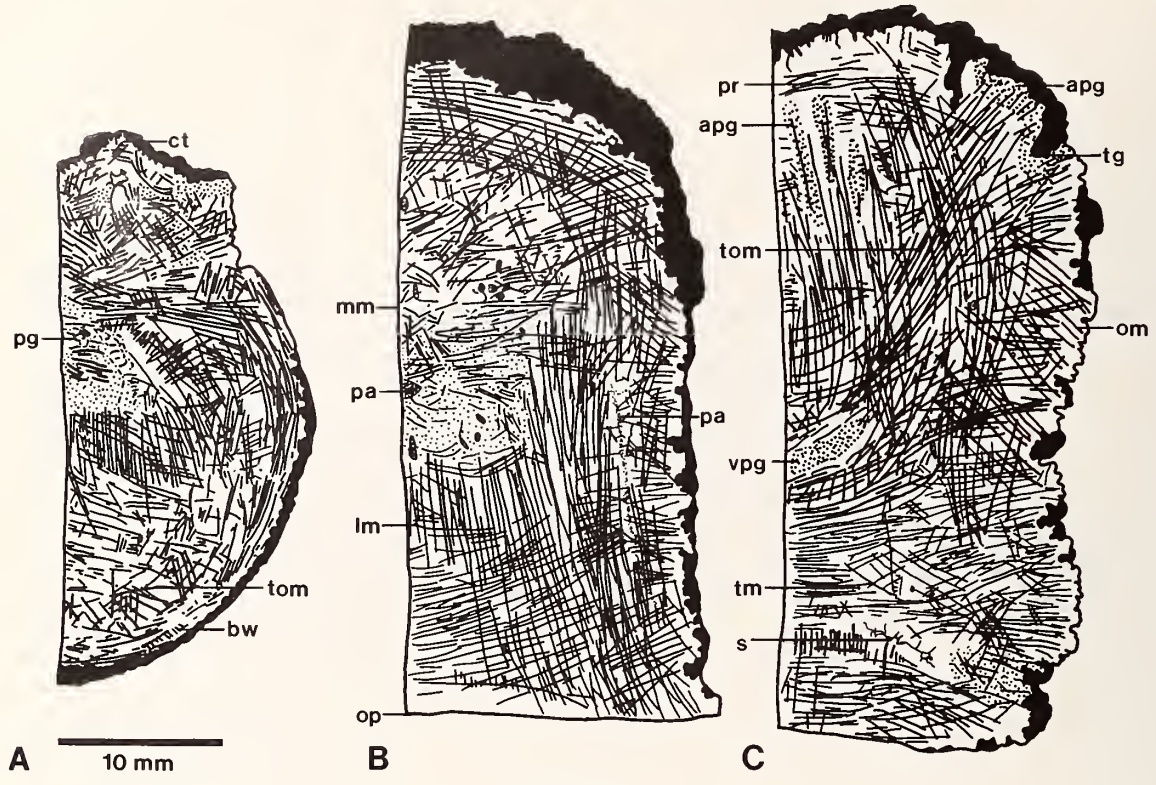

Figure 4

Camera lucida drawing of the musculature in frontal sections of a female *Busycon contrarium*. See Figure 2 for section locations in foot and stippling explanation. Anterior is at top of figure. A is more dorsal, C more ventral. Solid shading = epithelium on outer surface; apg = anterior pedal gland; bw = body wall musculature; ct = cephalic tentacle; lm = longitudinal muscle; mm = cut margin at midline of foot; om = oblique muscle; op = cut surface of operculum site; pa = pedal artery; pg = pedal ganglion; pr = propodium; s = sole; tg = transverse groove; tm = transverse muscle; tom = transverse oblique muscle; vpg = ventral pedal gland.

in the columellar muscle and 2.6 to 4.4 μm near the pedal epithelium.

Pedal Musculature of *Haliotis kamtschatkana*

Like the foot of *Busycon contrarium*, the foot of *Haliotis kamtschatkana* is composed of two distinct portions, the columellar region and the tarsos (Figures 7, 8). Unlike the situation in *Busycon*, however, the tarsic region in *Haliotis* surrounds the columellar region anteriorly, posteriorly, and laterally. The central core of the foot is composed of the hypertrophied right columellar muscle, which has its origin on the broad ventral surface of the shell and inserts on the sole epithelium. Thus, the long axis of the muscle is oriented perpendicular to the animal's anteroposterior axis. The majority of the muscle fibers in the columellar region lie in dorsoventral bundles. Dispersed among these are bundles of radial muscle fibers, and distributed through and around these two systems is a third system of concentric circular muscle fibers (Figures 7–9). The circular muscles are distributed around the periphery of the columellar region, while the radial muscles are more concentrated near its center. Some of the circular muscles may be helically oriented, wrapping the columellar muscle region in a discontinuous sheath of helically oriented muscle bundles. At least some of the radial muscle fibers are oriented in a direction oblique to, rather than strictly perpendicular to, the long axis of the columellar muscle.

Sagittal and transverse sections through a *Haliotis* foot show that the columellar region is bordered by the thick muscle bundles of the tarsos (Figure 10A), which radiate from their origin on the shell and divide into smaller and smaller branches that eventually penetrate the pedal epithelium at the sides and sole (Figures 7, 8, 11, 12). At the outer edge of the columellar muscle, these bundles branch into smaller bundles whose muscle fibers pass directly dorsoventrally through the foot and insert at the sole epithelium. Distal to these bundles, smaller branches spread slightly more laterally and become interspersed with the branches of neighboring bundles (Figure 11). At the sides of the foot, these finer branches spread laterally and ventrally, and penetrate the epithelium at oblique angles (Figure 12). Posteriorly, some of the smaller branches extend

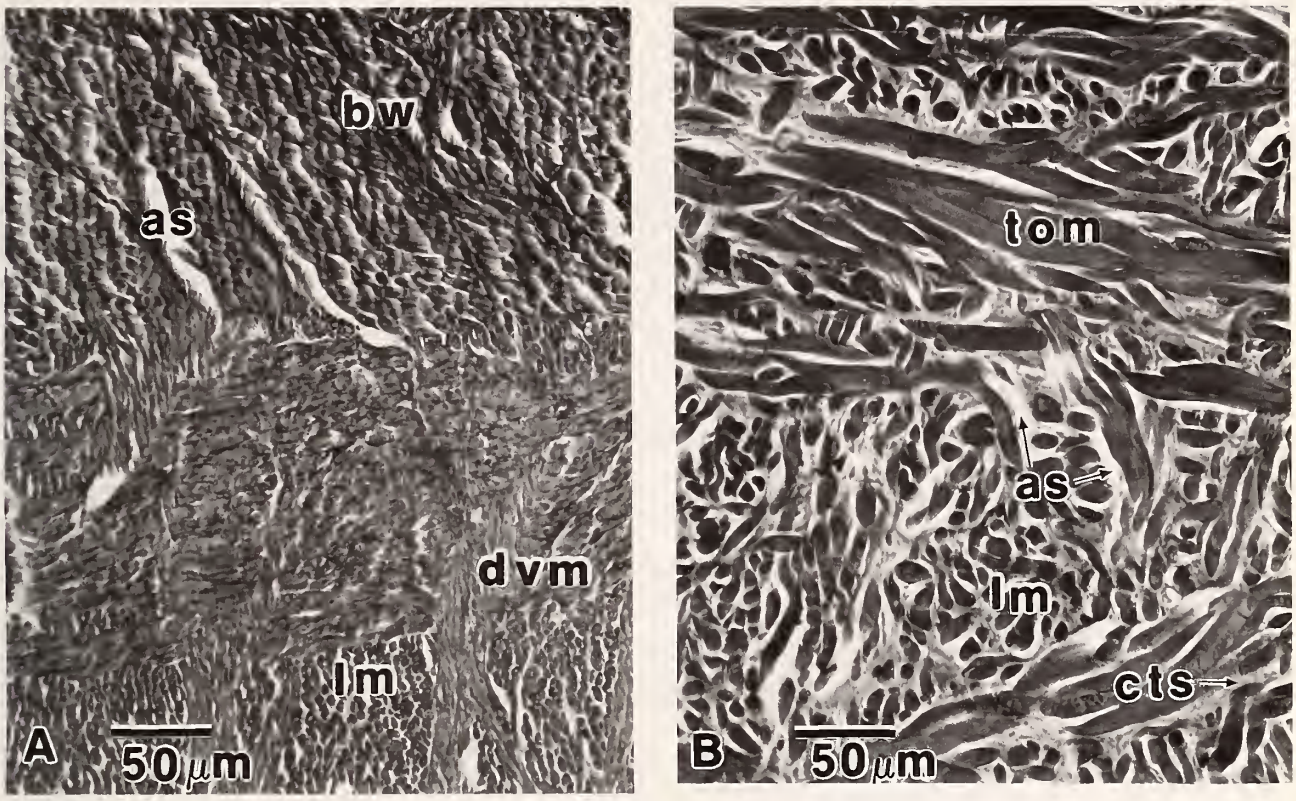

Figure 5

Photomicrographs of details from a section of the columellar muscle region of *Busycon contrarium*. Specimen was frozen in liquid nitrogen while crawling, fixed in glutaraldehyde-formalin, and stained with Milligan trichrome stain. A. Dorsal body wall. B. Thick muscle fibers of the interior of the muscle. Note than A and B have the same scale and show artificial spaces caused by paraffin embedding. as = artificial space; bw = body wall musculature; cts = connective-tissue sheath; dvm = dorsoventral muscle; lm = longitudinal muscle; tom = transverse oblique muscle.

almost horizontally, so that they fill the posterior portion of the foot with oblique, dorsoventral, and anteroposterior muscle fibers. In addition to these muscle fibers, the ventral portion of the sole contains some isolated transverse or obliquely transverse muscle fibers that appear not to be a part of the branching systems.

Pedal Connective Tissue

All of the muscle fibers of *Busycon* and *Haliotis* are wrapped in connective-tissue sheaths. These sheaths are quite distinct in sections stained with Mallory or Milligan trichrome, in which muscle is red and connective tissue is blue or blue-green (Figure 10). In fact, the foot is virtually solid muscle wrapped in connective-tissue sheaths (Figures 5, 6, 10–13). When viewed with polarized light microscopy, these sheaths are birefringent, indicating that they are anisotropic (Figure 13), and that the preferred orientation of the molecules composing the sheaths is parallel to the long axis of the muscle fibers. Preliminary information from amino acid analysis (performed on samples of *Busycon* and *Haliotis* pedal tissue by Dr. John Abernathy of the Duke University Department of Pathology) indicates by its imino acid content that the sheaths have a collagen component. Scanning electron microscopy (SEM) of muscle from *Haliotis* indicates that the sheaths are composed of parallel arrays of collagen fibers that are oriented parallel to the long axis of the muscle fibers they surround (Figure 14).

Within the columellar region of both species, the bundles of muscle fibers are wrapped in thin connective-tissue sheaths (Figures 5, 10). Virtually no other extracellular connective tissue is present. In the tarsic region, on the other hand, as the individual fibers within the bundles become smaller, the connective-tissue sheaths become thicker (Figure 10B, C), and the amount of extracellular connective tissue, both sheaths and seemingly unorganized matrix, increases towards the periphery of the foot (compare, for example, Figure 10 with Figure 12). The fine ramifications that insert at the sole are probably individual muscle fibers and are embedded in a dense connective-tissue matrix.

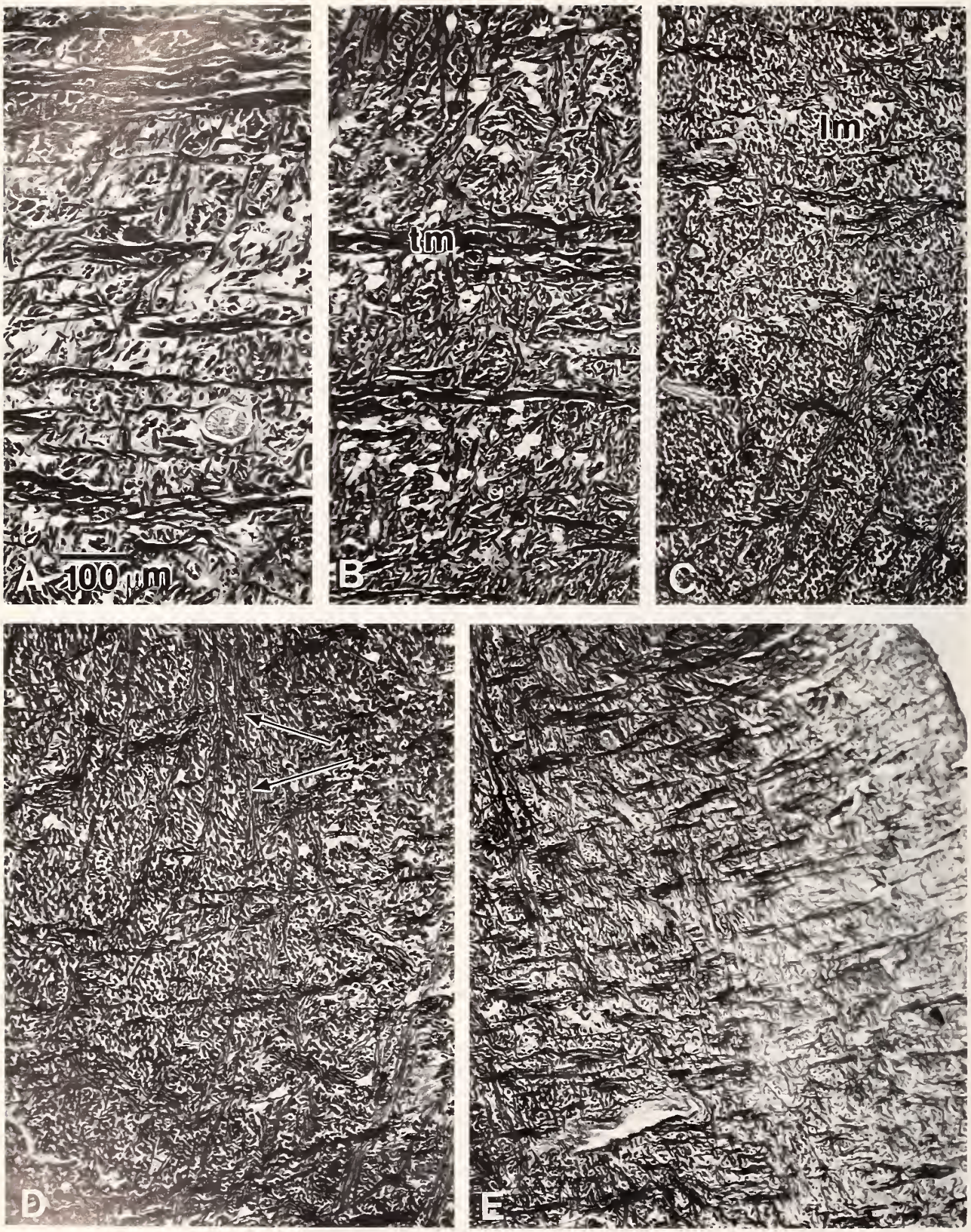

Figure 6

Photomicrographs from different areas of a 5-µm-thick transverse section through the tarsos of *Busycon contrarium* illustrating the decrease in muscle bundle size as the bundles spread from the interior (A) to the lateral epithelium (E) of the foot. Specimen prepared as in Figure 5. Note the branching of the dorsoventral (D, arrows) and transverse (E) muscle bundles. lm = longitudinal muscles; tm = transverse muscles.

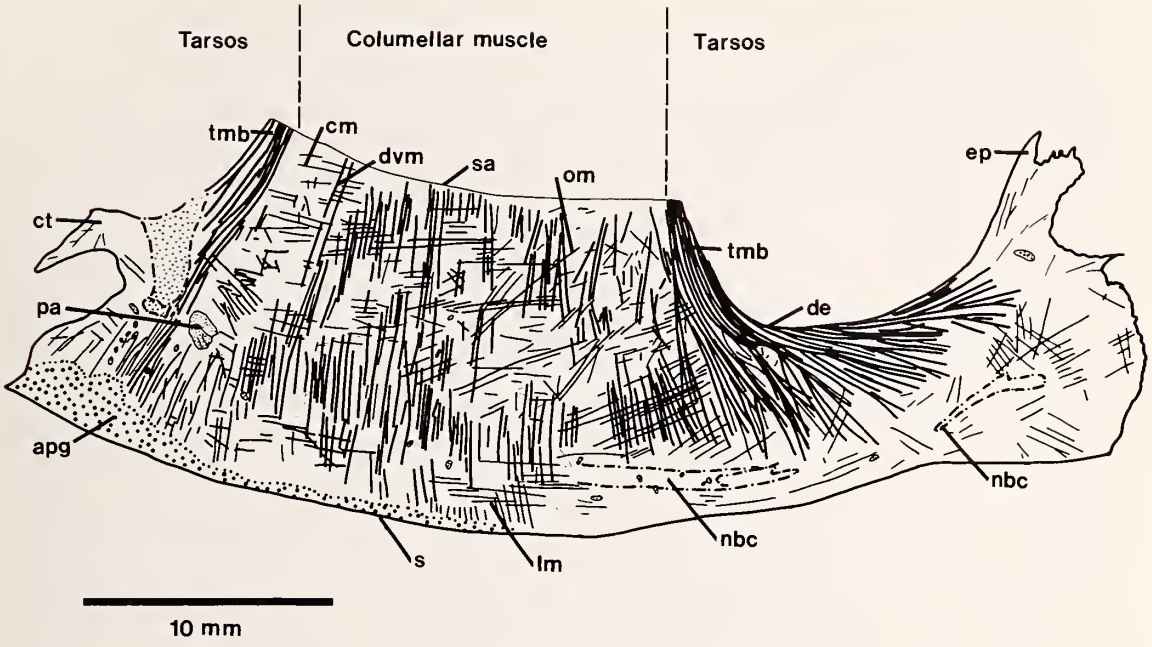

Figure 7

Camera lucida drawing of the musculature in a mid-sagittal section of a *Haliotis kamtschatkana* head-foot. Stippling as in Figure 2. apg = anterior pedal gland; cm = circular muscle; ct = cephalic tentacle; de = pedal dorsal epithelium; dvm = dorsoventral muscle; ep = epipodium; lm = longitudinal muscle; nbc = nerve and blood vessel channel; om = oblique muscle; pa = pedal artery; s = sole; sa = cut surface of shell attachment site; tmb = tarsic muscle bundles.

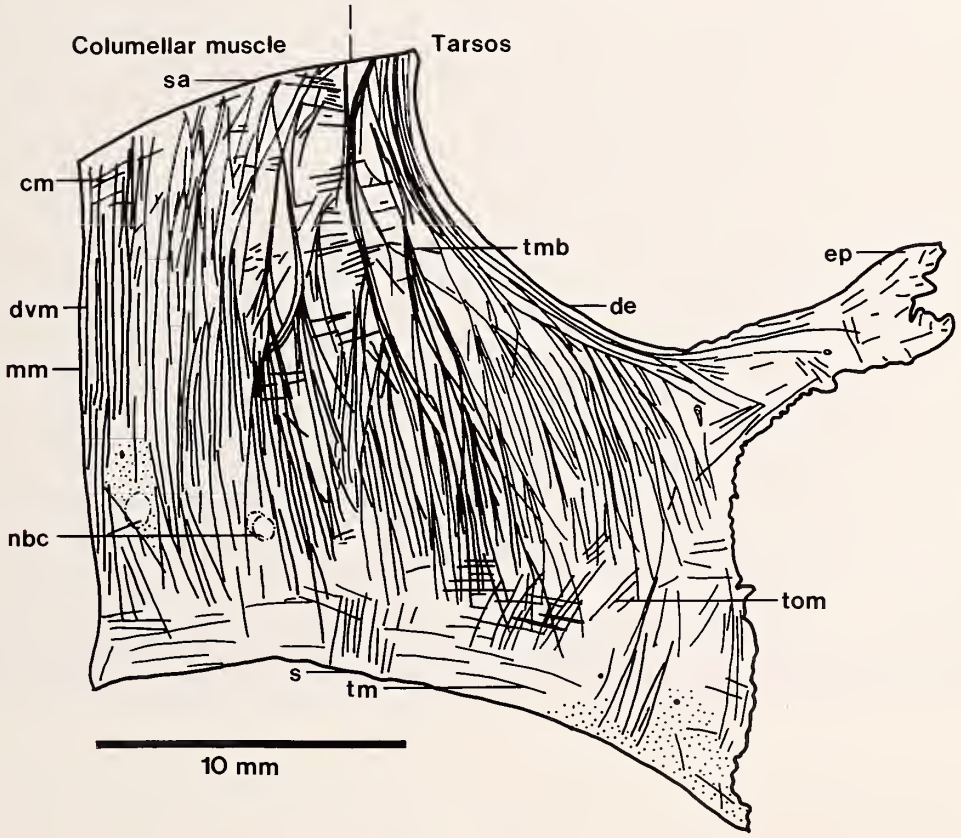

Figure 8

Camera lucida drawing of the musculature in a mid-transverse section of *Haliotis kamtschatkana*. Stippling as in Figure 2. cm = circular muscle; de = pedal dorsal epithelium; dvm = dorsoventral muscle; ep = epipodium; mm = cut margin at midline of foot; nbc = nerve and blood vessel channel; s = sole; sa = cut surface of shell attachment site; tm = transverse muscle; tmb = tarsic muscle bundles; tom = transverse oblique muscle.

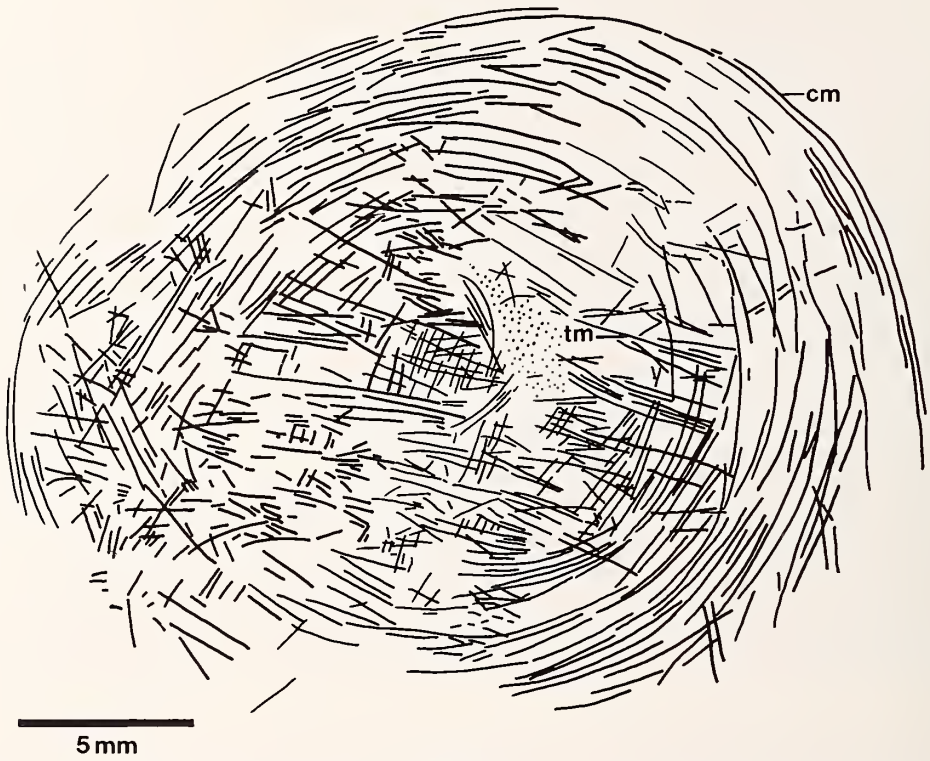

Figure 9

Camera lucida drawing of the musculature in a frontal section of the columellar muscle region of *Haliotis kamtschatkana*. The left side of the section is anterior and slightly more dorsal than the right. cm = circular muscle; tm = transverse muscle.

DISCUSSION

General Pattern of Pedal Muscular Organization

In both *Busycon contrarium* and *Haliotis kamtschatkana,* the foot consists of two distinct regions, the columellar muscle region and the tarsos. The columellar region consists primarily of muscle fiber bundles that are oriented parallel to the long axis of the muscle. In *Busycon,* this is a longitudinal direction in the expanded foot, in which the columellar muscle connects the columella with the operculum. In *Haliotis,* the major axis of the columellar region is dorsoventral, as is the majority of the muscle fibers comprising it. In addition, the columellar region of both species contains muscle bundles that are oriented perpendicular to the long axis of the muscle in at least two directions. In *Busycon,* these muscles are oriented in the oblique diagonal and radial directions; in *Haliotis* they are arranged in circles around the columellar muscle and in the radial directions as well.

In contrast to the columellar region, the tarsic region consists of bundles of muscle fibers that branch and change direction as they extend from their origins to their insertions. They form a complex three-dimensional network of interconnecting contractile fibers. The bundles become finer and finer as they approach the periphery of the foot and become more and more deeply embedded in the connective tissue of the ventral and lateral extremities. It is not clear at the light microscope level whether the decrease in bundle size is due to a decrease in cell diameter, a decrease in the number of cells per bundle, or both.

The Relationship Between Structure and Function

The structural differences between the two regions of the foot are reflected in their functions. The columellar muscle is primarily involved in producing major body movements and changes in shape and posture: protraction, retraction, twisting, elevating and lowering the shell, and clamping onto the substrate. Pressures generated by the forceful contraction of the columellar muscle in *Busycon* and *Haliotis* are quite large (over 3 kPa) and rapid (Voltzow, 1986). The functional system of a columellar muscle containing fibers that are arranged in a three-dimensional antagonistic network appears to be a fundamental one for prosobranch gastropods (Brown & Trueman, 1982; Trueman & Brown, 1985; Voltzow, 1986; Kier, 1988). Contraction of the bundles whose long axes are parallel to the long axis of the muscle results in retraction of the snail into its shell, as in *Busycon,* or in a reduction of the distance between the body and the substrate, as in *Haliotis*. More muscle fibers have this orientation than any other in the foot; their contraction appears

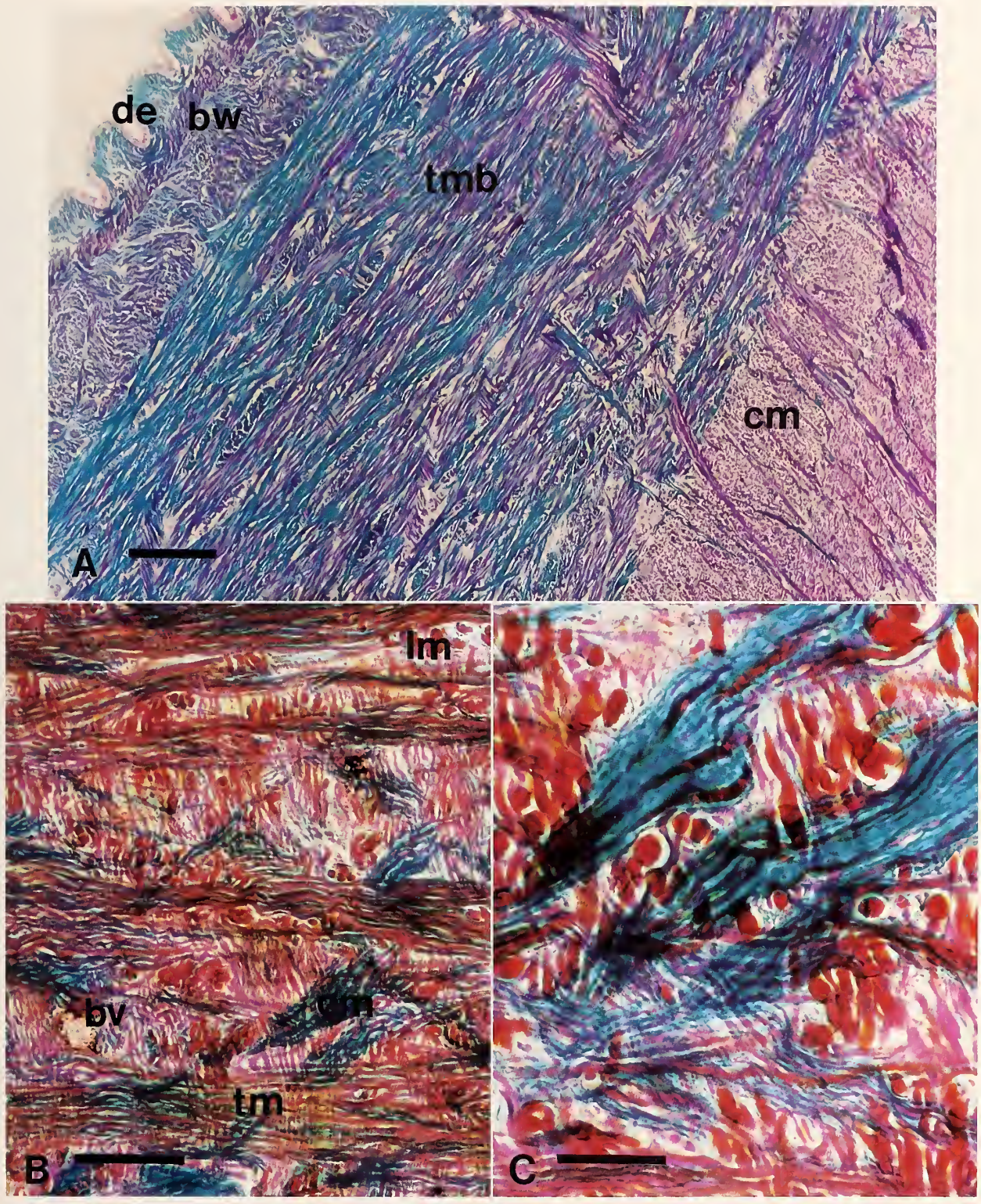

Figure 10

A. Photomicrograph of a 7-μm-thick sagittal section through the edge of the foot of *Haliotis kamtschatkana* showing the pedal epithelium and body wall musculature (upper left), the tarsos (center), and the columellar muscle region (lower right). Specimen was fixed in glutaraldehyde-formalin, embedded in Paraplast, and stained with Milligan trichrome stain. Muscle is red; connective tissue is blue. Scale bar = 200 μm. B. Photomicrograph of a 10-μm-thick transverse section through the transition between the columellar muscle region and the tarsos of *Busycon contrarium*. Transverse muscles at the top of the figure lie at the ventral edge of the columellar region. Specimen prepared as in Figure 5. Scale bar = 100 μm. C. Detail from section shown in B. Scale bar = 50 μm. bv = blood vessel; bw = body wall musculature; cm = circular muscle of the columellar region; de = dorsal pedal epithelium; lm = longitudinal muscle; om = oblique muscle; tm = transverse muscle; tmb = tarsic muscle bundles.

Figure 11

Photomicrograph of branching muscle bundles from a 5-µm-thick sagittal section of the tarsic region of *Haliotis kamtschatkana*. Specimen was narcotized with magnesium chloride, fixed with glutaraldehyde-formalin, embedded in JB-4, and stained with toluidine blue. Note the absence of artificial spaces.

to be the most forceful action the foot undergoes. Assuming that the columellar muscle has a constant volume, then if the major retractor muscles relax, contraction of the transverse, radial, or circular bundles will result in protraction or an increase in the distance between the shell and the substrate. The circular muscle of *Haliotis* would be particularly effective in lifting the shell above the substrate. In addition, at least some of the circular and transverse fibers appear to be helical. If they are arranged in left- and right-hand helices, then these muscles could also bring about the twisting action described in *Haliotis* and a similar twisting movement I observed in *Busycon*. The muscle fibers of the columellar region appear to play little or no part in the fine motor function of the rest of the foot. The

Figure 12

Photomicrograph of muscle fibers inserting at the sole epithelium from a 5-μm-thick sagittal section of the tarsos of *Haliotis kamtschatkana*. Specimen prepared as in Figure 11. Note that the lighter areas within the section are filled with connective tissue and are not artificial spaces. bw = body wall musculature; cts = connective-tissue sheath; lm = longitudinal muscle; om = oblique muscle; s = sole.

locomotor waves of *Haliotis*, for example, are restricted to the outer edges of the foot and do not pass through the portion of the sole where the columellar muscle inserts.

The tarsic musculature is involved in the fine movements of locomotion and food manipulation. Local contractions of the tips of several bundles probably produce the locomotor waves, which are accompanied by local fluctuations in pressure (VOLTZOW, 1986). By controlling the number of branches within a bundle and the number of bundles recruited, a gastropod should have a great deal of control over its fine motor functions. Over its entire course, a bundle may change directions, starting out with a dorsoventral orientation and eventually having an oblique or transverse orientation. The splitting of the bundles probably permits greater flexibility and variability in the movement of the foot. A large movement may be effected by

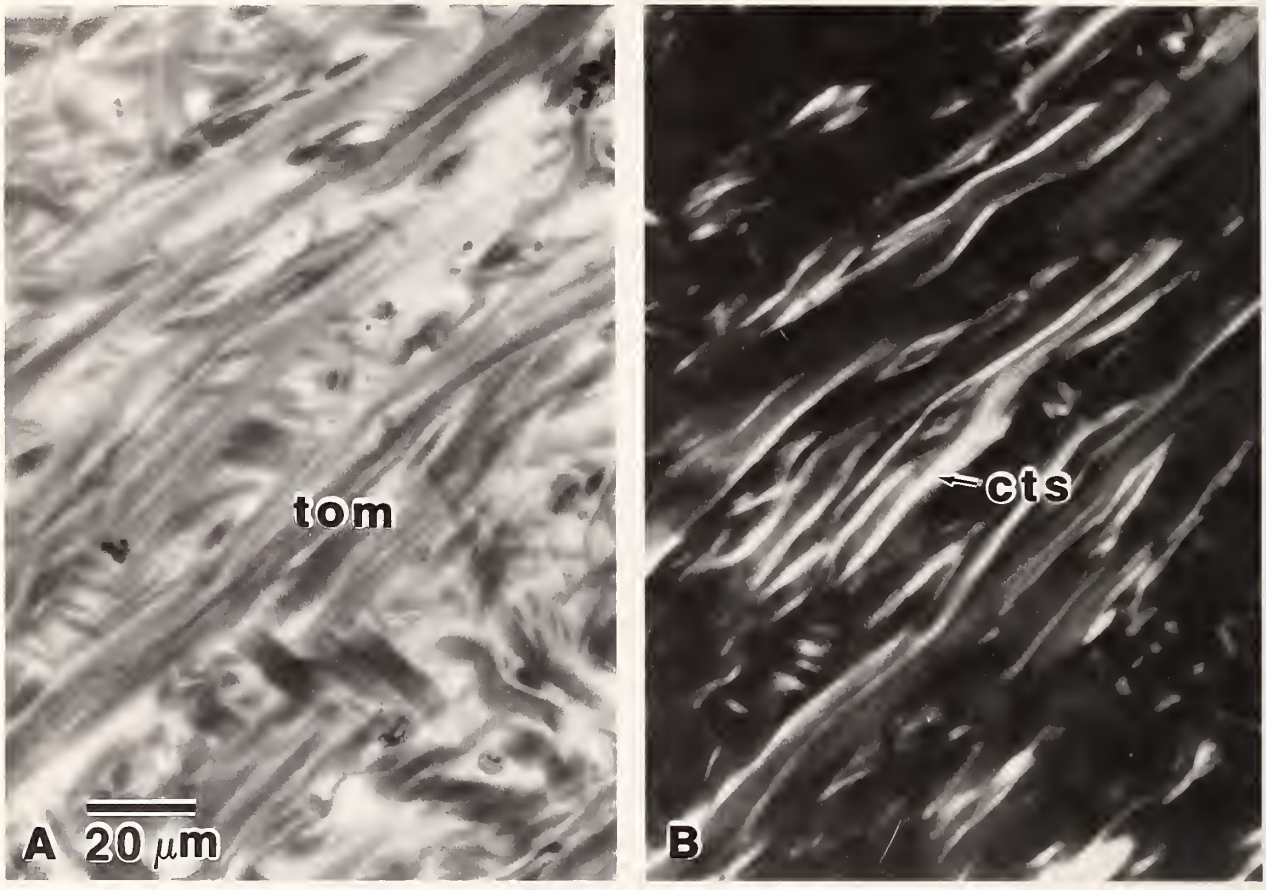

Figure 13

Photomicrographs taken with non-polarized (A) and polarized (B) light of muscle fibers and their connective-tissue sheaths from a 5-μm-thick sagittal section through the tarsic region of *Haliotis kamtschatkana*. Specimen prepared as in Figure 11. JB-4 is not birefringent, and the stain in the muscle fibers interferes with the birefringence, so that only the connective-tissue sheaths are visible with polarized light microscopy. cts = connective-tissue sheath; tom = transverse oblique muscle.

simultaneous contraction of all of the muscle fibers of several bundles. Finer movements should require only a few of the finest branches to be recruited.

Similar networks of branching bundles of muscle fibers have been noticed in the feet of several species of gastropods. WEBER (1926), for example, observed that in *Nassarius mutabilis* (=*Nassa mutabilis*) the muscle bundles divide into finer and finer units so that when they reach the connective tissue of the sole, they are broken up into individual fibers. ROGERS (1969) described the foot muscle of *Helix aspersa* Müller as arranged in bundles that "interweave to form a complex mesh." SCHMIDT (1965) noted that the functional changes of the form of the foot in *Helix pomatia* depend upon the lattice structure of the musculature. He stressed that the foot be analyzed as a functional system, a muscular antagonism system ("*muskularen Systemantagonisten*"), rather than as a set of isolated muscle fibers.

The Role of the Connective Tissue in Pedal Function

Essential to the meshworks of both the columellar muscle region and tarsos are the connective-tissue sheaths surrounding the muscle fibers. In the columellar region, the sheaths are relatively thin; in the tarsos, the sheaths increase in thickness as the bundle diameters decrease until individual muscle fibers are embedded in a dense matrix of connective tissue.

The connective tissue system has, until now, been omitted from studies of pedal functional morphology. While the details of its attachments to the muscle fibers and its ultrastructure are still unclear, the connective tissue system undoubtedly plays an important role in pedal function. At the gross level, the connective tissue contributes to the tough but flexible form of the foot and gives the foot its stretchy, elastic properties. As sheaths of oriented fibers around the muscle, the collagen provides each muscle with its own

tendon, and probably helps transmit forces from one portion of a bundle to another. Antagonism between opposing bundles could be aided by the anastomosis of the collagen fibrils between the sheaths of neighboring muscle cells. The mechanism for this rests, in part at least, with the connective tissue connection between the muscle fibers and their sheaths, and between the antagonizing muscle bundles and their attachments. The increase in volume fraction of connective tissue at the periphery of the foot probably provides the increased flexibility and deformability of this region, because the action of each muscle fiber can be amplified by the passive action of the connective tissue around it.

Bundles of muscle fibers bound together by connective tissue similar to those described here for *Busycon* and *Haliotis* were observed in the foot of *Patella* by DAVIS & FLEURE (1903). SCHMIDT (1965) observed that the muscle fibers of *Helix pomatia* were surrounded by fibers that were collagenous or that greatly resembled collagenous fibers: single fibrils had crossbands at regularly discernible distances of about 63 nm (collagen has a characteristic periodicity of approximately 67 nm [WOODHEAD-GALLOWAY, 1980]). Unfortunately, he did not discuss the collagen orientation with respect to the muscle fiber. Each muscle fiber in the feet of *Neritina reclivata* and *Thais rustica* has a connective-tissue sheath (GAINEY, 1976). In the foot of *Polinices lewisi* (Gould), BERNARD (1968) saw that all the muscles were ensheathed with collagen-reaction type connective tissue. SMINIA (1972) saw a network of connective-tissue fibers around the muscle fibers of *Lymnaea stagnalis*. These fibers stained with aniline blue and by silver impregnation, so they are probably collagen and/or reticulin (procollagen) fibrils. Silver impregnation staining of *Lymnaea* sections also indicated to PLESCH *et al.* (1975) that each muscle cell was surrounded by a fine network of reticulin fibers. PLESCH (1977) found that the muscle cells of *L. stagnalis* are organized in a meshwork and are anchored to the connective tissue surrounding them by hemidesmosome-like structures. She made no mention of fiber angles, either between collagen fibers or between collagen and muscle fibers. Her study is the only ultrastructural information available on the connections between gastropod pedal muscle fibers or between the fibers and their connective-tissue sheaths. Although all of these authors observed the connective-tissue sheaths, none made any attempt to understand their function. In addition, none of the models of gastropod locomotion discussed in the introduction make any mention of connective tissue. More information about the fine structure and precise orientation of the collagen sheaths and their connections is necessary to understand how the connective tissue transmits the forces of contraction in the foot.

Scanning electron microscopy of muscle from the foot of *Haliotis kamtschatkana* and amino acid analysis of both gastropod species indicate that the sheaths around the muscle cells are composed of parallel arrays of collagen very similar to those illustrated in vertebrate tissue by NAGEL (1934, 1935), BORG & CAULFIELD (1980), and WINEGRAD & ROBINSON (1978). If the sheaths described for *Busycon* and *Haliotis* are composed of parallel arrays of collagen fibers oriented strictly parallel to the long axis of the muscle fibers they surround, they may be acting as a tendon around the muscle fiber to prevent its over extension. The sheaths may also serve to link one set of muscle fibers with another, distributing the force of contraction or extension, as has been proposed for similar vertebrate systems by NAGEL (1934, 1935), and WINEGRAD & ROBINSON (1978). In addition, I propose that these connective-tissue sheaths provide the mechanism by which one set of muscle fibers can directly antagonize another by transmitting compressive and tensile forces.

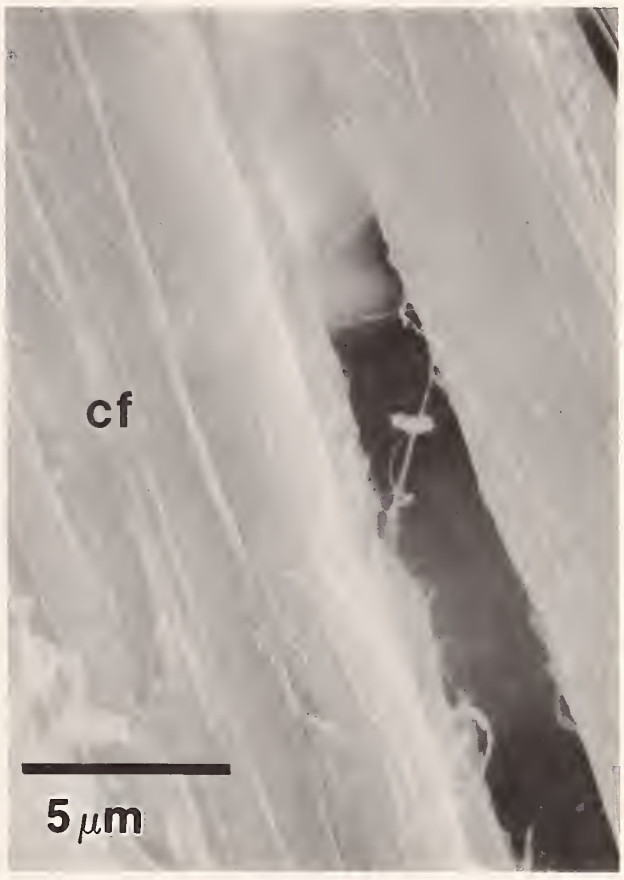

Figure 14

Scanning electron micrograph of the columellar muscle of *Haliotis kamtschatkana* showing collagen fibers forming a sheath around the muscle fibers. cf = collagen fiber.

The Prosobranch Foot as a Hydrostatic Skeleton

The gastropod foot has traditionally been viewed as a hydrostatic organ. A hydrostatic skeleton is one in which

body fluid provides the means by which the contractile elements are antagonized (CHAPMAN, 1958). Although, as Chapman has pointed out, any incompressible fluid that transmits pressure in all directions can function as a hydrostat, the usual candidate is a large, fluid-filled space, such as the coelom of annelids or the coelenteron of cnidarians. In models of gastropod locomotion, the circulatory system, or hemocoel, is usually considered the hydrostat. Thus, the transmission of pressure via the hemocoel and its role in muscular antagonism have become a central tenet in accounts of locomotor wave propagation and burrowing (TRUEMAN, 1983).

The pedal circulatory systems of *Busycon* (VOLTZOW, 1985) and *Haliotis* (CROFTS, 1929; BOURNE & REDMOND, 1977) consist of distinct arteries and veins. Only at their finest ramifications do the vessels appear to lack any walls of their own; here they are delimited by the muscle and connective tissue surrounding them. In both species, the columellar muscle region and tarsos receive blood from separate branches of the anterior aorta. There appears to be no mixing of blood between the two portions of the foot. The most extensively vascularized area is the region just dorsal to the sole, where an elaborate system of small, branching vessels penetrates the channels between the muscles and connective tissue. Even in this region, however, the blood occupies only approximately 7% of the total volume of the expanded foot (VOLTZOW, 1985).

Most histological techniques cause shrinkage and distortion that tend to occlude cavities or to create artificial ones. In sections in which the tissue was fixed in Bouin or Zenker and embedded in paraffin, small spaces appeared between the muscle fibers. These spaces resembled those that previous authors have labeled hemocoel in similarly prepared sections of the gastropod foot. In sections fixed in the osmotically controlled glutaradehyde-formalin fixative and embedded in paraffin, the spaces were somewhat reduced (*e.g.,* Figure 5). Those embedded in JB-4 essentially lacked these spaces (*e.g.,* Figure 11). From these sections it is clear that the foot is predominantly solid muscle wrapped in connective-tissue sheaths. Although I have not studied the species described by others, I have examined the feet of at least 20 species of chitons and gastropods using vascular injections and dissections (VOLTZOW, 1985, and personal observation). Although TRUEMAN & BROWN (1976) have demonstrated that an extensive pedal hemocoel does exist in *Bullia,* I believe that much of what has been identified as hemocoelic space in the feet of other marine prosobranchs is actually artifact due to the shrinkage associated with fixation and paraffin embedding.

The arrangement of the muscles in the columellar muscle makes it possible for them to antagonize each other. Thus, the columellar muscle is a muscular-hydrostat (*sensu* KIER & SMITH, 1985). Although the blood in the tarsos does not usually occupy a large central cavity, it does probably contribute to the overall turgor of the foot by filling the many fine vascular channels. The tarsos is not as solid a muscular organ as is the columellar muscle. Instead, the tarsic regions of *Busycon* and *Haliotis* are hydrostatic systems in which the role of the body fluid is intermediate between that of a classic hydrostatic cavity and muscular-hydrostat.

Throughout the diversity of species of prosobranchs, the extent of vascularization of the tarsic region appears to be quite variable. Limpets such as *Patella vulgata* and *Tectura scutum* (Rathke, 1833) (=*Notoacmaea scutum*), for example, have a very reduced pedal circulatory system; the entire foot is essentially solid muscle (JONES & TRUEMAN, 1970; VOLTZOW, 1988). TRUEMAN & BROWN (1976), on the other hand, have identified a large blood-filled space in the foot of *Bullia digitalis.* In addition, water-filled, or aquiferous, systems have been described for several species of naticids (BERNARD, 1968; RUSSELL-HUNTER & RUSSELL-HUNTER, 1968; RUSSELL-HUNTER & APLEY, 1968). The tarsos, therefore, probably spans the entire range of possible hydrostatic systems, from the solid muscles of limpets to more fluid-dependent systems such as the highly inflated foot of *Bullia.*

Evolutionary Trends in the Functional Morphology of the Prosobranch Foot

There have been at least two major trends in the evolution of the prosobranch foot. First, there has been a repeated convergence upon the limpet shape. In each case, it appears that the muscle system is organized into a series of paired muscle bundles that extend dorsoventrally and spread diagonally as they approach the sole, so that a transverse section of a limpet foot closely resembles that of a monoplacophoran or polyplacophoran (VOLTZOW, 1988). This organization most likely increases the ability of the limpet to adhere to hard substrates, which are the characteristic limpet habitats.

The second major trend is less obvious, but I believe that there has been a tendency toward a reduction of the columellar muscle and a corresponding increase of the tarsic system in non-limpet prosobranchs. The prosobranchs are traditionally divided into three subclasses: Archaeogastropoda, Mesogastropoda, and Neogastropoda. This classification roughly corresponds to the sequence in which the members of the subclasses appear in the fossil record. MILLER (1974b) found that archaeogastropods tend to use rhythmic pedal waves only, mesogastropods use all patterns except diagonal ditaxic waves, and the neogastropods use rhythmic, arrhythmic, and ciliary locomotion. Although prosobranch gastropods are an extremely diverse group, in general, archaeogastropods are characterized by a globose, low spired shell, round shell aperture, and a round sole. Neogastropods tend to have a shell with an elongate aperture and have reduced or lost their opercula. Mesogastropods tend to be intermediate (FRETTER & GRAHAM, 1962; MILLER, 1974a, b; MCNAIR *et al.,* 1981; GAINEY & STASEK, 1984), although many neogastropods and mesogastropods show convergence in shell form (SIGNOR,

1985). The shift in shell shape and locomotor type from archaeo- to meso- and neogastropods is usually attributed to a habitat expansion from rocky substrates to sand and mud (YONGE & THOMPSON, 1976). Thus, through evolutionary time, a trend appears, from an operculated, round foot that uses distinct, simple muscular waves to a more elongate shell with a narrow aperture and a foot that lacks an operculum and uses more complex, less distinct waves. Of course, as with any generalization of evolutionary trends there are many exceptions, but certainly, the tarsos of *Busycon* is much more complex and performs a greater range of movements than the tarsos of *Haliotis*. In the feet of non-limpet gastropods that lack an operculum, the columellar muscle loses its integrity and divides into bundles that spread to the anterior, posterior, and ventral parts of the foot (BRACE, 1977). Increases in functional plasticity of the neogastropod foot could be accomplished by the integration of these columellar bundles with the already extensive ramifications of the tarsic muscle fiber arrangement. Thus the entire foot would have the flexibility of the tarsos combined with the force of the columellar muscle. It should be possible to examine more feet and follow the changes that the columellar muscle and tarsos have undergone in the various families to see if this trend has in fact occurred.

SUMMARY

(1) Dissections and histological sections show that the feet of *Busycon contrarium* and of *Haliotis kamtschatkana* consist of two distinct regions, the dorsal or central columellar muscle region and the ventral or peripheral tarsos. Both regions are composed of muscle bundles wrapped in connective tissue sheaths.

(2) The columellar region contains bundles of large-diameter (usually greater than 5 μm) muscle fibers wrapped individually in thin connective-tissue sheaths. Most of the bundles are oriented parallel to the long axis of the muscle. Additional bundles cross the region and form a lattice of radial, transverse, and longitudinal muscle fibers.

(3) The tarsos contains bundles of muscle fibers that divide into smaller and smaller branches as they extend from the dorsal to the ventral portions of the region. As the branches become smaller, the thickness of the connective-tissue sheaths surrounding them becomes greater. The muscles of the tarsos comprise a three-dimensional network of interwoven muscle fibers, mostly of small diameter (usually less than 5 μm), that pass through the foot in oblique, transverse, dorsoventral, and anteroposterior directions.

(4) The muscle bundles of the columellar region appear to be responsible for the major movement of the foot into and out of the shell. They also function to twist the shell from side to side and to lift and lower it relative to the substrate.

(5) The branching muscles of the tarsos are responsible for the fine movements of wave propagation, prey manipulation, and egg capsule shaping.

(6) The connective-tissue sheaths probably play an important role in the antagonism of one muscle set by another.

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LITERATURE CITED

ABBOTT, R. T. 1974. American seashells. 2nd ed. Van Nostrand Reinhold: New York. 663 pp.

BEKIUS, R. 1972. The circulatory system of *Lymnaea stagnalis* (L.). Neth. Jour. Zool. 22:1–58.

BERNARD, F. R. 1968. The aquiferous system of *Polinices lewisi* (Gastropoda, Prosobranchiata). Jour. Fish. Res. Board Can. 25:541–546.

BIEDERMANN, W. 1905. Studien zur vergleichenden Physiologie der peristaltischen Bewegungen. II. Die locomotorischen Wellen der Schneckensole. Pflügers Arch. Gesamte Physiol. Menschen Tiere 107:1–56.

BORG, T. K. & J. B. CAULFIELD. 1980. Morphology of connective tissue in skeletal muscle. Tissue & Cell 12:197–207.

BOURNE, G. B. & J. R. REDMOND. 1977. Hemodynamics in the pink abalone, *Haliotis corrugata* (Mollusca, Gastropoda). I. Pressure relations and pressure gradients in intact animals. Jour. Exp. Zool. 200:9–16.

BRACE, R. C. 1977. The functional anatomy of the mantle complex and columellar muscle of tectibranch molluscs (Gastropoda: Opisthobranchia), and its bearing on the evolution of opisthobranch organization. Philos. Trans. Roy. Soc. Lond. B, 277:1–56.

BROWN, A. C. & E. R. TRUEMAN. 1982. Muscles that push snails out of their shells. Jour. Molluscan Stud. 48:97–98.

CARLSON, A. J. 1905. The physiology of locomotion in gasteropods. Biol. Bull. 8:85–92.

CARRIKER, M. R. 1951. Observations on the penetration of tightly closing bivalves by *Busycon* and other predators. Ecology 32:73–83.